THE UMZAMBA FORMATION AT ITS TYPE SECTION, UMZAMBA ESTUARY (PONDOLAND, TRANSKEI), THE AMMONITE CONTENT AND PALAEOGEOGRAPHICAL DISTRIBUTION

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(With 5 figures and 3 tables)

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ABSTRACT

Detailed collecting at the type section was undertaken to determine the exact age of the Formation and to determine whether more than one faunal zone is present. Faunal analysis based on ammonites shows that the age of the Formation at the type section ranges from Middle Santonian to Lower Campanian. The ammonoid faunas at the type section of the Umzamba Formation in Pondoland were compared with those of the False Bay region of Zululand, and it was found that certain morphotypes, e.g. oxycones, compressed evolute forms, and serpenticones are more dominant in the shallower water transgressive environment of Pondoland, presumably as a reflection of different living conditions in the two areas.

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INTRODUCTION

Although the presence of Cretaceous sediments in the vicinity of the Umzamba River Estuary (Pondoland, Transkei) has been known since at least 1824, the exact age and the question of whether or not a succession of distinct faunal associations is recognizable have long been disputed (Baily 1855; Griesbach 1871; De Grossouvre 1901; Rogers & Schwarz 1902; Woods 1906; Du Toit 1912, 1920, 1954; Van Hoepen 1920, 1921, 1965; Plows 1921; Spath 1921b, 1922, 1953; Rennie 1930; Haughton 1963, 1969; Kennedy & Klinger

1975). On the basis of the fauna and flora described by Baily (1855), Griesbach (1871), Chapman (1904, 1923), Woods (1906), Lang (1906), Broom (1907), Spath (1921d, 1921b), Van Hoepen (1920, 1921, 1965), Renine (1930, 1935), Smitter (1956), Little (1957), Mädel (1960), Müller-Stoll & Mädel (1962), Dingle (1969), and Kennedy & Klinger (1977a, 1977b 1979), ages varying from Albian to Maastrichtian were postulated, the prevalent idea being that the Formation was of Senonian age (i.e. Coniacian to Campanian).

Failure to arrive at a decisive conclusion may be ascribed mainly to lack of present stratigraphic control, and/or lack of current knowledge of the systematic affinities and stratigraphic ranges of some of the fossil taxa.

Aided by the extensive monographical studies of the Madagascar ammonoid faunas by Colliginon (1928 onwards), his series Atlas des fossiles caracteristiques de Madagascar (ammonites), and by the authors' preliminary biozonation for southern Africa (Kennedy & Klinger 1975), a new attempt was made to fill this gap in our current knowledge. For this purpose a detailed sampling programme was undertaken by one of the authors (H.C.K.) in 1974. However, due to circumstances beyond the authors' control, results of this investigation could not be published earlier and consequently parts thereof were disclosed elsewhere (Klinger & Kennedy 1977: Cooper 1977).

Finally, the apparent faunal differences between northern Zululand and Pondoland are examined briefly to determine their extent and probable causes.

DESCRIPTION OF THE EXPOSURES

Descriptions of the exposures at and near the Umzamba Estuary are provided in varying degrees of detail by Garden (1855), Griesbach (1871), Rogers & Schwarz (1902), Du Toit (1912, 1920), Plows (1921), Gevers (in Rennie 1930) and Kennedy & Klinger (1975), that of Plows (1921) being the most complete. Apart from details of the ammonoid succession at the type section, little else can be added to these general accounts. The lithologies encountered may be described briefly as follows:

The Cretaceous strata overlie Ordovician? quartzites belonging to the Table Mountain Group unconformably with a slight seaward dip of the order of two to four degrees. The basal beds are conglomeratic, consisting of abundant sandstone and lydianite pebbles set in an arenaceous matrix. Large logs, chelonian scutes and other reptilian remains, comminuted shell material, selachian teeth, and beaulitid ammonites are locally common in these basal beds. Higher up in the sequence, lithologies become finer-grained, consisting essentially of alternating layers of grayish-green, fine-grained silts, and coarsergrained, shelly or sandy concretionary horizons. Some of the concretionary layers yield abundant fossils, and sections of gigantic inoceramids, more than a metre in diameter, are conspicuous. Fossils in the silty horizons are generally preserved as internal moulds, whereas those in the concretionary horizons retain

the original shell material. The majority of ammonites extracted from the concretionary horizons were embedded horizontally.

The most complete exposure is on the northern side of the estuary (Figs 1-2), named the Umzamba Cliff by Plows (1921, pl. 8 (fig. 3)). This is Gevers's (in Rennie 1930) 'first locality' and the authors' (Kennedy & Klinger 1975) locality 1. Griesbach's (1871, fig. 5) locality was probably taken about 100 m north-east of here (Fig. 3). Details of the section here vary considerably due to landslides and heavy surf action at the base of the cliff (see Rogers & Schwarz 1902: 40; Plows 1921: 60).

The Umzamba Cliff is here referred to as locality A (see Figs 3-4). Beds A3 and A7 are the levels of the prominent caves remarked upon by the early workers. These result from the collapse of the soft, silty beds between hard, concretionary layers. Horizons below Bed A8 can be easily reached from the base of the cliff by climbing on rubble from landslips. Higher horizons can be reached by scaling the cliffs or by taking a footpath over the top of the hill and then climbing down the cliff (see also Gevers 1977 for anecdotal details).

During low tide, foreshore platforms are exposed north-east of locality A for more than a kilometre along the beach. Due to the abundance of silicified tree trunks, this locality is known as the 'Petrified Forest' and is indicated as such on tourist and topographic maps. Most of the larger logs appear to be orientated in an east-north-east direction, presumably paralleling the Cretaceous shoreline. The exposures are in horizons below those seen at locality A, and are here referred to as locality B.

Locality C is situated on the southern side of the estuary (Plow's 1921 Right Bank), and extends for some distance along the coast, but the latter is only poorly exposed at low tide (see Rogers & Schwarz 1902; 40). Strata even lower down in the succession than those found at locality A and B are exposed here, but the actual contact with the underlying basement rocks was not exposed during the authors' visits. Large boulders of quartzite derived from the Ordovician? Table Mountain Group are exposed on the NW side of the estuary, but one or two metres of sand covered the actual contact. Approximately 10 m of sediment are exposed at locality C. The highest bed, Bed C11, probably corresponds to Bed 3 at locality A.

THE AGE OF THE UMZAMBA FORMATION

In determining the age of the Umzamba Formation at the type section, the ammonoid zonation compiled for Madagascar by Collignon (1966, 1969) and the provisional one compiled for Natal and Zululand by the authors in a slightly modified form (Kennedy & Klinger 1975) (Tables 1 and 2 respectively) are employed.

The base of the section

The lowermost fossiliferous units are Bed C4 and the foreshore outcrops in the northern part of locality B. Occasional Baculites capensis Woods, rare

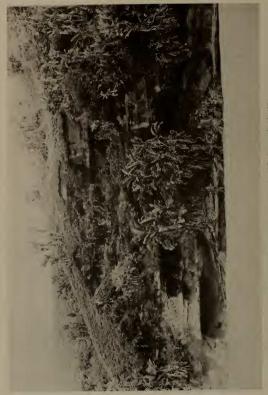


Fig. 1. The main exposure at Umzamba, Umzamba Cliff, photographed in 1974. Mr Johannes Nonyane is at the foot of the cliff for scale.

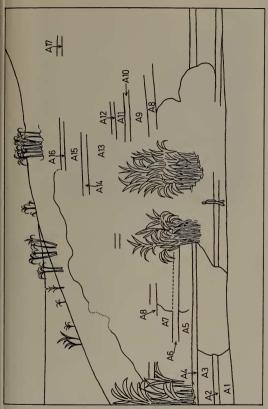


Fig. 2. Drawing of Umzamba Cliff to illustrate units as referred to in the text and in Figure 4.



Fig. 3. Section at Umzamba about 100 m to the north of the main exposure shown in Figure 1. This appears to be the site on which Griesbach (1871 (fig. 5)) based his section.

Gaudryceras varicostatum Van Hoepen, Texanites umzambiense Klinger & Kennedy and Scaphites sp. occur here.

The authors had originally considered (Kennedy & Klinger 1971, 1975) that the base of the Umzamba Formation was of Coniacian age on the basis of the reference of Muniericeras cricki Spath (1921b, 1922) (of which Barroisiceras umzambiensis van Hoepen 1965 (Fig. 7A) is a synonym) to the Coniacian collignoniceratid genus Subprionotropis. Since most of the above listed species are typically Santonian forms, this determination became open to question, and the authors would now suggest that this species is better referred to the homoeomorphic genus Lehmaniceras Collignon, 1966 (see also Klinger & Kennedy 1977: 103; Cooper 1977: 16). Van Hoepen's specimen was collected from an unrecorded horizon on the southern side of the Umzamba Estuary at locality C. Apart from Pondoland, Lehmaniceras is known only from Madagascar where it is relatively abundant in the Middle Santonian.

The association of Texanites umzambiense Klinger & Kennedy with Baculites capensis Woods is related to that of Plesiotexanites olivetiforme Klinger & Kennedy and Baculites capensis occurring in the first division of the Santonian in Zululand. In Madagascar, Baculites capensis occurs in the Lower

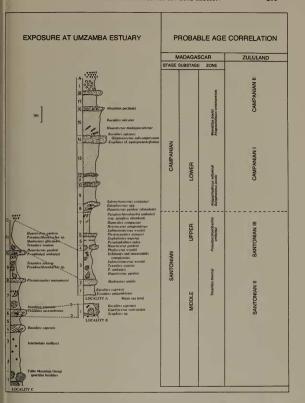


Fig. 4. Stratigraphic section at Umzamba, including Umzamba Cliff, here marked A, the foreshore beach exposures north of A, here marked as B, and the section on the southern side of the estuary, here marked C.

TABLE I

Ammonoid zonation for Madagascar as compiled by Collignon; after Collignon 1966 and 1969.

MIDDLE				Basal zone of Pachydiscus lamberti					
LOWER CAMPANIAN		Smortoniceras	1	Zone of Menabites boulei and Anapachydiscus arrialoorensis	Subzone of Termierella lenticularis Subzone of Rabeiella orthogonia				
	leni	Menabites & Submortoniceras & Bererella		Zone of Karapadites karapadensis	Subzone of Scaphites reesidei Subzone of Maorites aemilii				
	Hauericeras gardeni	Bevahites	Eulophoceras	Zone of Anapachydiscus wittekindi and Eulophoceras jacobi	Subzone of Hourcquiella bererensis Subzone of Besairiella besairiei				
		Ber	F	Basal unit with Neogauthiericeras zafimahovai					
UPPER		Zone of Pseudoschloenbachia umbulazi							
MIDDLE				Zone of Texanites hourcgi					
LOWER				Zone of Texanites oliveti					

TABLE 2

Provisional ammonoid succession for Natal and Zuuland as compiled by the authors (1975), here presented in slightly modified form to accommodate new data.

CAMPANIAN	Menabites (Australiella) abundant in lower part. Some appear to range throughout together with Bevalutes spp. Baculites sudcatus is abundant throughout while pachydiscids become common in the higher part, e.g. A. wittekindi, A. artialourensis						
CAMPANIAN	Submortoniceras woodsi and related forms are common; other ammonites include Bevahites and Menabites. Hauericeras gardeni, Pseudoschloenbachia. Bostrychoceras and diplomoceratids. The local base of the stage is drawn below the level of abundant Submortoniceras						
SANTONIAN	Hauericeras gardeni is abundant; the remainder of the fauna is as in Santonian II and is relatively scarce.						
SANTONIAN	Abundant Plesiotexanites stangeri and varieties. Texanites sontoni, Texanites spp. Houericeras and Pseudoschleenbachia occur, as do Eupachydisens? Hyphantoceras and diplomoceratids						
SANTONIAN	Texanites oliveti, Plesiotexanites stangeri densicosta and sparsicosta. Hauericeras gardeni, Pseudoschloenbuchin sp Pseudophyllites indra. Korapadites?, Eupachydiscus? Sp. Gaudryceras spp. Myphantoceras ps. and diplomoceratids. The base of the stage is drawn at the level of the appearance of Texanites sensu strictu in numbers						
CONIACIAN	Abundant baculitids ornamented only by growth striae. Also ammonites resembling Pseudoschloenbachia primitiva Collignon and Scaphites.						

and Middle Santonian. Gaudryceras varicostatum occurs as low as the second division of the Coniacian of Zululand, but is also recorded from the Lower Santonian of Madagascar (Collignon 1966: 3).

On the basis of these ranges, it seems quite certain that the basal beds are of Santonian age, and probably uppermost Lower to Middle Santonianin thesense of Collignon (1966) and equivalent to the authors' first or second divisions, probably the latter, of the Zululand Santonian.

Top of the succession

The uppermost ammonite-bearing beds exposed, Beds A14 and A15 (probably the equivalent of Gevers's (in Rennie 1930) Bed T) yield Baculties sulcatus (Baily), Hauericeras madagascariense Collignon (Fig. 5B), Glyptoxoceras subcompressum (Forbes) and Scaphites cf. aquisgranensiformis Collignon. Hauericeras madagascariense has a very restricted range in Madagascar, occurring only in the upper part of the Lower Campanian zone of Menabites boulei and Apapachydiscus arrialoorensis (see Collignon 1961, 1969; and Table 1 herein). Comparisons with Zululand at this interval are tenuous, but Baculties sucleatus is comparable with Baculties vanhoepent Venzo, as discussed earlier (Klinger & Kennedy 1977: 73–74) and is indicative of the second division of the Campanian in Zululand. The absence of Menabites s.1. species which characterize this horizon in Zululand, however, is puzzling.

The uppermost exposed beds at the Umzamba Cliff are thus provisionally dated as uppermost Lower Campanian in the sense of Collignon (1969) and tentatively the second division of the Zululand Campanian sensu Kennedy & Klinger (1975).

Subdivision of the sequence

The ammonites collected in situ from the remainder of the sequence exposed at the Umzamba Estuary are shown in Figure 4. Apart from a thin zone of rolled and encrusted clay pebbles and hiatus concretions in Bed A5, which may represent a very short break in deposition, no evidence could be found of a major sedimentological interruption within the Umzamba Formation. It may thus be assumed that deposition was virtually continuous.

Bed A7 yields abundant Pseudoschloenbachia umbulazi umbulazi (Baily), P. umbulazi (Baily) griesbachi van Hoepen, and P. umbulazi (Baily) spinifera van Hoepen (all probably conspecific). All three 'subspecies' occur together, but P. umbulazi spinifera appears to become more abundant towards the top of the Bed. Hauericeras gardeni (Baily) is also very abundant. This association corresponds to the third division of the Santonian in Zululand, and the Upper Santonian zone of Pseudoschloenbachia umbulazi in Madagascar. Eulophoceras tenue van Hoepen, E. umzambiense van Hoepen and other Eulophoceras species (all probably conspecific) occur together with Submortoniceras condamyi near the contact of Beds A7 and A8. In Madagascar the base of the Campanian is drawn immediately below the first occurrence of Eulophoceras, whereas it is



Fig. 5. A. Lehmaniceras cricki (Spath, 1921). (= The holotype of Van Hoepen's 1965: 161, pl. 6 and text-fig. 2a Barroisiceras umrambiensis. From the southern side of the Umzamba Estuary (herein locality C) at an unknown horizon (see Van Hoepen 1965: 162). Geological Survey SAS-P1093. ×1.

B. Hauericeras madagascariense Collignon, 1961. This is the specimen collected by Gevers from his horizon 'T' at the Umzamba Cliff (herein locality A), probably horizon A15, being associated with specimens of Baculites sulcatus Baily on reverse side. South African Museum SAM-7043. x 0,75.

drawn in Zululand below the first occurrence of abundant Submortoniceras. It seems reasonable to draw the contact between the Santonian and Campanian Stages at the contact between Beds A7 and A8. It should be pointed out, however, that Submortoniceras appears slightly earlier in Pondoland than in Madagascar.

The paucity of ammonites from above Bed A7 at the type section appears to be due more to physical difficulties encountered in collecting in higher sections of the cliff rather than real differences.

Scaphites cf. aquisgranensiformis in Bed A14 is comparable with S. aquisgranensiformis Collignon, which occurs in the subzone of Scaphites reesidei at the boundary between the Zone of Menabites boulei and Anapachydiscus arrialorensis and the Zone of Karapadites karapadensis of the Lower Campanian of Madagascar.

COMPARISON OF THE PONDOLAND AND ZULULAND AMMONOID FAUNAS

The authors (Klinger & Kennedy 1977: 104; 1980) and Spath (1921b: 53) had previously pointed to the apparent differences between the ammonoid faunas of Pondoland and those of biostratigraphically equivalent sediments further north at Umkwelane Hill and in the False Bay region of Zululand.

A detailed comparison of the faunas of Pondoland with those of Durban, Richards Bay, Umkwelane Hill, and Zululand must await a complete revision of all the ammonoid faunas, but preliminary results are given here in Table 3. The paucity of the faunas in the Durban and Richards Bay and to a lesser extent the Umkwelane Hill regions as shown in the table are primarily due to lack of sufficient exposures, rather than real differences. Furthermore, the absence of some Pondoland species in Zululand may be partially due to our inability to recognize the generally small Pondoland species as the nuclei of larger species occurring in Zululand. This latter discrepancy is not applicable to the Texanitinae, which generally grow to very large size, especially in Pondoland.

Despite these shortcomings, the picture that emerges is not one of total geographic separation, but rather one of concentration of certain shell morphotypes in specific areas. Very good examples of this are the oxyconic pseudoschloenbachiids and Eulophoceras spp., the compressed evolute Hauericeras gardeni (Baily) and also the serpenticonic rounded Plesiotexanites stangeri (Baily). Examination of the Van Hoepen Pondoland collections in the Transvala Museum (Pretoria) and personal collection at the type section, shows that Pseudoschloenbachia and Hauericeras can be counted by the thousands, as compared to numbers well below the hundreds in biostratigraphically equivalent strata in Zululand. Known specimens of Eulophoceras from Pondoland number about fifty, whereas the number from Zululand is well below ten. Similarly, only two tentative specimens of Plesiotexanites stangeri (Baily) are known from the False Bay region of Zululand, whereas it is relatively common in Pondoland.

TABLE 3

Distribution of ammonoid taxa at Umzamba, Durban, Richards Bay, Umkwelane Hill and

Distribution of ammonoid taxa at Umzamba, northern 2	Zululand		s Bay, U	mkwelan	e Hill and
Abbreviations					
Absent		mmon undant) = 10-50) = >100
			BAY	60	
	PONDOLAND		e s	UMKWELANE	9
SPECIES	J.V	Z	CZ.	頁	3
SPECIES	Ž	DURBAN	RICHARDS	8 4	ZULULAND
	PO	na	RIC	E G	zn
Phylloceras (H.) woodsi woodsi van Hoepen .	0	_	_	_	
Partschiceras umzambiense (van Hoepen)	R	_	_	_	_
Tetragonites superstes van Hoepen	0	_	_	_	_
Saghalinites cala (Forbes)	R	_	_	_	
Saghalinites nuperus (van Hoepen)	O	_	_	_	R
Pseudophyllites indra (Forbes)	R	_	_	_	R
Pseudophyllites teres (van Hoepen)	R	_	_	_	_
Gaudryceras varicostatum van Hoepen (= G. cinctum Spath 1922)	R				
(= G. cinctum Spath 1922)	R				
Anagaudryceras subsacya (Marshall)	_	R	_	_	_
Anagaudryceras subtilineatum (Kossmat)	R		_	_	_
Vertebrites kayei (Forbes)	R	_	_	R	_
Gaudryceras denseplicatum (Jimbo)					
(= amapondense van Hoepen)	R	_	_	_	R
'Heteroceras' amapondense van Hoepen	R	_	_	_	R-O
Pseudoxybeloceras amapondense van Hoepen .	R	_	_	_	?
Glyptoxoceras compressum (Forbes)	R	_	R	_	R
Hoploscaphites spp	R-O	_	O-C	o-c	?
Baculites capensis Woods	0-C	O-C	0-0	C C	A A
Baculites bailyi Woods	O C			_	?
Damesites compactum van Hoepen	R				
Desmophyllites simplex van Hoepen	R			_	_
Desmophyllites crassa (van Hoepen)	R	_	_	_	_
Hauericeras gardeni (Baily)	A	R	0	O-C	С
Hauericeras madagascariense Collignon	R	_	_	_	_
Natalites spp	O-C	_	_	_	_
(including N. natalensis Spath, N. acutico-					
status Spath, N. faku van Hoepen, N. africanus					
van Hoepen, N. similis Spath)					
Parapuzosia haughtoni Spath	R		_	R	_
Pachydiscus simplex van Hoepen	R R	_	_	_	
Pachydiscus untafunensis Spath Pachydiscus antecursor van Hoepen	R				
Eulophoceras spp	O-C	?R		_	R
(including Eulophoceras natalense Hyatt,	0.0				
'Spheniscoceras' africanum Spath, 'S' tenue					
Spath, 'S' minor Spath, 'Pelecodiscus' ama-					
pondense van Hoepen, 'P' umzambiense					
van Hoepen)					
Pseudoschloenbachia spp	Α	_	0	0	0-C
(including P. umbulazi (Baily), P. pseudo-					
fournieri Spath, P. papillata Spath, P. gries-					
bachi Spath)	D				
Texanites umzambiense Klinger & Kennedy .	R R				R
Texanites presoutoni Klinger & Kennedy	C		R	R	Ĉ
Texanites texanus s. 1	Ř				Ř
Submartaniagras woodsi (Snath)	R	R	R	R	O

Submortoniceras woodsi (Spath) . . . Submortoniceras condamyi Collignon . Plesiotexanites stangeri (Baily) . . . Plesiotexanites matsumotoi Klinger & Kennedy Lehmaniceras cricki (Spath) Other species, such as Texanites soutoni (Baily), Submortoniceras woodsi (Spath) and S. condamyi (Collignon) are common to both areas, though subtle differences exist as discussed earlier (Klinger & Kennedy 1980) meriting separation at subspecific level. In the smooth lytoceratid forms the picture is somewhat obscure due to limited numbers (Kennedy & Klinger 1977b). Saghalinites nuperus (van Hoepen) and Pseudophyllites indra (Forbes) are common to both Zululand and Pondoland, but are numerically superior in Pondoland. Pseudophyllites teres (Marshall) is poorly known and has so far been recorded from Pondoland only.

Phylloceratids are also restricted in numbers in Pondoland, but both known species, Phylloceras (Hypophylloceras) woodsi wan Hoepen and Partschiceras umzambiense van Hoepen have so far not been recorded from the False Bay region of Zululand (Kennedy & Klinger 1977a).

Details on the pachydiscids are still in preparation but show no distinct trends, neither do the gaudryceratids (Kennedy & Klinger 1979).

Amongst the heteromorphs, Baculites capensis Woods and B. bailyi Woods are common to both Zululand and Pondoland, whereas the Pondoland species, B. sulcatus (Baily), has a possible equivalent in Zululand in B. vanhoepeni Venzo (Klinger & Kennedy 1977). 'Heteroceras' amapondense van Hoepen (= Anaklinoceras stephensoni Collignon 1966) is relatively rare, but is known from both areas, as also, apparently are species of Pseudoxybeloceras and Glyptoxoceras. The scaphitids have not been studied sufficiently for detailed analysis.

The fact that species such as Texanites soutoni, Submortoniceras woodsi, S. condanyi, Pseudoschloenbachia umbulazi and Hauericeras gardeni occur in all major outcrop areas, ranging from Umzamba, through Durban, Richards Bay and Umkwelane Hill to the False Bay region of Zululand, clearly precludes the presence of an impenetrable physical barrier, and supports the authors' previous views (Klinger & Kennedy 1977: 104) of open marine connection between the areas. One of their previous views, however, that the biostratigraphically equivalent strata in Zululand were probably not well exposed (Klinger & Kennedy 1977: 104) now appears erroneous in view of the above data.

It has been suggested recently (see Cooper 1977: 32) that trophic resources increase during transgressions, which in turn leads to population explosions of certain favoured species. In the case of the diachronous southwards-extending Umzamba Formation Santonian transgression (Klinger & Kennedy 1977), these favoured species appear to be the oxyconic pseudoschloenbachiids and Eulophoceras spp, the compressed evolute Hauericeras gardeni and the serpenticonic Plesiotexanites stangeri.

Due to the abundance of specimens, a high degree of splitting into various morphotypes was applied to species (see Van Hoepen 1921; Spath 1922). The authors would suggest that it will be possible to reduce the various 'species' or variants of *Pseudoschloenbachia* and *Eulophoceras* to a single species each, as has been done in the case of *Plesiotexanites stangeri* (Baily) (Klinger & Kennedy 1980).

(A comparable situation to that at Umzamba occurs in Zululand following the Lower Coniacian transgression (Kennedy & Klinger 1971). Here the sediments are dominated by the oxyconic Proplacenticeras 'species' P. umkwelanense (Etheridge), P. subkaffrarium (Spath) and P. kaffrarium (Etheridge) and very evolute serpenticonic peroniceratids belonging to the groups of Peroniceras tridorsatum (Schlüter), P. dravidicum (Kossmat), P. westphalicum (Schlüter) etc. Klinger, et al. (in prep.) suggest that the Proplacenticeras 'species' ranging from the completely smooth P. umkwelanense through P. subkaffrarium with undulating flanks to the distinctly umbilically spinose P. kaffrarium all belong to one variable species. A similar simplification of peroniceratid systematics is also envisaged.)

The question which now arises, and for which the authors can find no specification answer, is why these particular morphotypes (oxycones, e.g. Pseudoschloenbachia; compressed evolute, e.g. Hauericeras; and serpenticoe, e.g. Plesiotexanites stangeri) proved to be so successful in terms of numbers in a shallow-water, transgressive environment and tended towards a certain degree of endemism and great intraspecific variation.

The wide global distribution of *Plesiotexanites stangeri* (Klinger & Kennedy 1980) clearly shows that these forms were not restricted to transgressive habitats only and were capable of substantial dispersal, but apparently preferred a shallower water transgressive milieu. It may be suggested that the shell types were hydrodynamically suited to this particular type of environment, but again specific explanations are lacking.

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